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THE INHERITANCE OF EYE COLOR IN MAN—
BROWN AND NONBROWN

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INTRODUCTION

THIS report is concerned with the inheritance of brown and nonbrown pigment in human eyes. No attempt is made to analyze the several eye-color patterns nor is any distinction made between the different shades of brown. The study is quantitative only insofar as quantity may be appraised by visual techniques without the aid of specialized measuring tools. The investigation was supported and the report is here published through aid from the Horace H. Rackham School of Graduate Studies, University of Michigan.

METHODS

All observations of eye color were made by myself in natural light. Although the light intensity varied considerably from day to day, the lighting generally was good. The amount of iris pigment was classified according to the following grades: 1, no brown pigment observable; 2, a trace of brown; 3, one-fourth brown; 4, one-half brown; 5, three-fourths brown; 6, a trace of nonbrown; and 7, completely brown. The analysis has given each of these grades equal rank even though this introduces a small error, since the difference (observationally) between grades 1 and 2 and between grades 6 and 7 is less than the difference between the other grades.

The data have been gathered from 107 families with a total of 212 children: (a) one child, forty-six families; (b) two children, thirty-nine families; (c) three children, twelve families; (d) four children, three families; (e) five children, four families; (f) six children, two families; and (g) eight children, one family. The racial ancestry of all families may be classified as North European. The family residence now is mainly in the central to east section of the Lower Peninsula of Michigan.

ANALYSIS OF DATA

The frequencies for the various eye-pigment grades in parents and in their children are given in Table I. The male children slightly outnumber the female children. Female parents are significantly darker eyed than are male parents (average grade $\bar{y} = 3.32$, $\sigma = 1.84$; $\bar{x} = 2.73$, $\sigma = 1.67$) and are somewhat more variable in eye color. Here σ refers to the standard deviation of the distribution: $\sigma^2 = 1/n \sum (x - \bar{x})^2$. Male children are darker eyed and more variable than are female children ($\bar{x} = 2.72$, $\sigma = 1.70$; $\bar{y} = 2.42$, $\sigma = 1.51$), and the children are lighter eyed and less variable than the parents. These sexual differences are not consistent and probably are ascribable to the sampling process rather than to genetic peculiarities.

The mating combinations ($P \times P$) and the grades of eye color in children (F) for each possible mating type are summarized in Table II. In terms of the mating possibilities presented by the population there is no evident homogamy in eye color. A person with a certain grade of eye color is no more likely to mate with a person having his own grade than with one having any other grade. This is shown both by the correlation coefficient ($r_{\sigma\varphi} = -.009$) and by the chi-square test ($\chi^2 = 27.82$; not significant for 36 degrees of freedom).

Among the children the statistical number of sibling pairs is 191; forty of these are female pairs, fifty-seven are male pairs, and ninety-four are male and female pairs. This statistical number is the sum of all possible sibling comparisons within a family. For example, in a family containing two male and two female children there are four male and female pairs, one male pair, and one female pair. One of the female pairs appears to be identical (Table III, Family 26). No other multiple births are recorded.

The parents range from twenty-two to fifty-four years of age and the children from three to twenty-eight years. There is no evident association between amount of brown pigment in the eye and the age of either parents ($r = .004$) or children ($r = -.074$). Further consideration of age will consequently be omitted.

The association between sex and amount of brown pigment in the iris is not significant among parents ($\chi^2 = 7.97$; $P = .30$) or among children ($\chi^2 = 5.40$; $P = .50$).

Within a family the following twelve statistical pairings may be tested. These pairings may be measured by the product-moment correlation (r), by the chi-square goodness of fit test (χ^2), by the probable significance (P), and by two additional statistics derived from the chi-square summations—mean square contingency (ϕ^2) and coefficient of mean square contingency (C).

1. ♂ parent—♀ parent. In these data there is no reported evidence of consanguinity between parents. In addition, insofar as may be determined from other measurements made on the families, such as blood

TABLE I
DISTRIBUTION OF BROWN SERIES EYE PIGMENT IN 107 FAMILIES

		Grades											
1		2		3		4		5		6		7	
No.	Per cent	No.	Per cent	No.	Per cent	No.	Per cent	No.	Per cent	No.	Per cent	No.	Per cent
Parents													
Male	29 27.10	30 28.04	14 13.08	19 17.76	9 8.41	2 1.87	4 3.74						
Female	17 15.89	34 31.78	15 14.02	14 13.08	12 11.21	5 4.67	10 9.35						
Children													
Male	33 30.00	32 29.09	12 10.91	9 8.18	17 15.45	4 3.64	3 2.73						
Female	33 32.35	34 33.33	14 13.73	9 8.82	6 5.88	4 3.92	2 1.96						

group, secretor and taste factors, traits of the dento-facial complex, etc., there is no evidence in any instance that legal parents are not the biological parents. The parents may be assumed to be unrelated and, as pointed out above, they show no likenesses in brown pigment in the iris that are not attributed to the sampling process.

2. ♂ parent—♂ offspring. The number of pairings is 110, $r = .673$, $\chi^2 = 132.60$, $P = .01-$, $\phi^2 = 1.1839$, and $C = +.736$. Four items in the father-son pairings appear unduly to magnify the χ^2 value. If these are extracted from the manifold table, χ^2 is reduced to 78.31, C to $+.648$, and r to $.564$; P remains significant at the $.01-$ level.
3. ♂ parent—♀ offspring. The number of pairings is 102, $r = .462$, $\chi^2 = 72.73$, $P = .01-$, $\phi^2 = .7130$, and $C = +.645$. One item is questionably erratic. Its removal reduces χ^2 to 58.00, C to $+.623$; r and P are not changed. The internal evidence from the correlation matrix indicates that r would be increased to about $+.51$ if a larger sample were used.
4. ♂ parent—offspring. There are 212 pairings, $r = .541$, $\chi^2 = 152.74$, $P = .01-$, $\phi^2 = .7205$, and $C = +.647$. Extraction of two items reduces χ^2 to 123.29 and C to $.628$; P remains at $.01-$. The value of r adequately describes the correlation matrix.

The analysis of amount of iris pigment in the male parent and in his offspring, treated both dependently and independently of sex, shows similarity which cannot be attributed to chance. Differences in the amount of similarity between father-son and between father-daughter are suggested by r , χ^2 , and C . Detailed examination of the manifold tables and correlation matrices indicates that the differences present may well be attributed to minor erraticisms within the samples. A reserved conclusion, then, is that the male parent's contribution to the eye color of his offspring is probably not differentiated according to sex.

5. ♀ parent—♂ offspring. There are 110 pairs, $r = .207$, $\chi^2 = 71.71$, $P = .01-$, $\phi^2 = .6460$, and $C = +.627$. The manifold table presents no irregularities which unduly influence χ^2 and its derived statistics. The correlation value given needs no correction.
6. ♀ parent—♀ offspring. The number of pairs is 102, $r = .291$, $\chi^2 = 54.37$, $P = .02$, $\phi^2 = .3477$, and $C = +.522$. Detailed examination of the manifold tables and correlation matrices suggests no changes in the values given.
7. ♀ parent—offspring. The number of associations is 212, $r = .242$, $\chi^2 = 79.55$, $P = .01-$, $\phi^2 = .3752$, and $C = +.522$. No distributional irregularities are evident.

The P values, consistently below the $.01$ level, indicate the associations in eye pigment between mother-son, mother-daughter, and mother-offspring to be real and not attributal to the operation of chance factors. The difference between the mother-son ($.207$) and mother-

daughter (.291) correlations is too small to warrant the conclusion of differential influence of sex, but is sufficiently large to suggest further consideration with more adequate data. These differences shown by the correlation are, however, contraindicated by χ^2 and C.

A comparison of the male parent-child associations with the female parent-child ones shows the former to be greatly in excess over the latter; the compared averages are: $r = .559$ and $.247$, $\chi^2 = 119.37$ and 68.54 , and $C = .676$ and $.580$, respectively. Two explanations may be offered: (a) the results are peculiar to this sample and would not be substantiated by a more extensive body of data; or (b) the statistical treatment involved in setting up parent-child pairs according to the number of children in the family may magnify or minimize unduly the true differences.

The first suggestion seems most reasonable. Reference to Table II shows very clearly that the division of the total sample into its several mating combination subgroups gives a series of very small samples no one of which is sufficiently large to permit highly refined appraisal. The largest subgroup, $P_2 \times P_2$, is represented by fifteen families containing only twenty-nine children, fourteen male and fifteen female. Furthermore, twenty-one of the possible twenty-eight $P \times P$ subgroups include five or fewer families each with nine or fewer children.

The second proposition has some merit. The discussion already has shown that in a body of data of this size the method of analysis permits a very small percentage of apparently irregular items to influence strongly the magnitude of r , χ^2 , and C. Aside from these difficulties there is no reason why the pairing method should, in itself, produce inaccurate results. In other words, care must be exercised when using statistics derived from small samples, regardless of the value of P.

8. Midparent—offspring. The midparent as used in this discussion is obtained by taking one-half of the sum of the grades for the male parents and the female parents. There are 212 pairs, $r = .590$, $\chi^2 = 206.75$, $P = .01$ —, $\phi^2 = .9752$ and $C = +.703$. Removal of two irregular items in the manifold table reduces χ^2 to 149.53 and C to .655; P remains significant at the .01 level, and r is unaffected. There is no important difference between the midparent-male offspring and the midparent-female offspring correlations ($r = .585$ and $.595$ respectively).

With the exception of the male parent-female offspring correlation, the midparent-offspring correlations are the highest of the intrafamilial pairings tested. This suggests a blending type of inheritance in the eye pigmentation.

9. ♂ sibling—♂ sibling. There are 57 pairs; $r = .490$, $\chi^2 = 67.33$, $P = .01$ —, $\phi^2 = 1.1812$, and $C = +.736$. One item is irregular. Its removal reduces χ^2 to 49.27 and C to .668; P remains at less than .01, and r is unaffected.
10. ♂ sibling—♀ sibling. There are 93 pairs, and all associations except that

attributal to four erratic items is of zero order. This result is unexpected and seems to be due to the sample used. At least, the findings should be verified by additional data before attempting explanation.

11. ♀ sibling—♀ sibling. There are 40 of these associations; $r = .498$, $\chi^2 = 76.78$, $P = .01$ -, $\phi^2 = 1.9195$, and $C = +.811$. Removal of one irregular item reduces χ^2 to 45.42 and C to .647; r and P are not affected.
12. Sibling—sibling. There are 191 pairs; $r = .275$, $\chi^2 = 77.33$, $P = .01$ -, $\phi^2 = .4049$, and $C = +.535$. No items are strikingly erratic, and the values given reflect largely the failure of association in ♂-♀ sibling pairs.

DISCUSSION

Two statistical methods for measuring association of intrafamilial pairs have been employed; product-moment correlation and the chi-square goodness of fit. Both techniques show within-family associations that are not attributal to chance. The correlations vary between $-.048$ and $+.673$ and

TABLE II

GRADES OF BROWN AND NONBROWN EYE COLOR IN CHILDREN OF 107 FAMILIES
NUMBER OF CHILDREN OF EACH GRADE FROM PARENTS OF EACH POSSIBLE MATING TYPE

Grades of Parents	Families		Grades of Eye Color of Children							
	Number	Per Cent	1	2	3	4	5	6	7	Average
1×1	6	5.61	17	1	1	...	...	...	...	1.16
1×2	10	9.35	13	11	2	...	...	...	...	1.58
1×3	4	3.74	3	3	3	...	...	...	...	2.00
1×4	9	8.41	9	5	...	2	2	...	...	2.06
1×5	4	3.74	2	3	...	...	1	...	...	2.17
1×6	3	2.80	2	4	...	...	1	...	...	2.14
1×7	4	3.74	...	4	...	1	...	...	1	3.17
2×2	15	14.02	9	17	1	1	1	...	...	1.90
2×3	7	6.54	1	5	7	...	...	...	...	2.54
2×4	9	8.41	4	2	3	4	3	2	1	3.52
2×5	4	3.74	...	2	3	1	1	...	...	3.14
2×6	2	1.87	...	...	2	1	...	...	...	3.33
2×7	2	1.87	2	1	...	...	...	2	...	3.20
3×3	3	2.80	...	...	...	2	1	...	...	4.33
3×4	4	3.74	1	...	2	3	1	1	...	3.75
3×5	5	4.67	1	3	2	1	...	...	...	2.43
3×6	0		...	...	...	...	...	...	...	
3×7	3	2.80	1	1	...	...	2	...	1	4.00
4×4	2	1.87	...	1	...	1	1	1	...	4.25
4×5	4	3.74	1	...	...	...	6	...	...	4.43
4×6	1	0.93	...	...	...	...	1	1	...	5.50
4×7	2	1.87	...	1	...	1	...	...	...	3.00
5×5	1	0.93	...	1	...	...	...	1	...	4.00
5×6	0		...	...	...	...	...	...	...	
5×7	2	1.87	...	1	...	...	2	...	1	4.75
6×6	0		...	...	...	...	...	...	...	
6×7	1	0.93	...	...	...	...	...	...	1	7.00
7×7	0		...	...	...	...	...	...	...	
Totals	107	99.99	66	66	26	18	23	8	5	2.58

average +.491; all but one is significant at the .01 level. Considerable differences are found between the several correlations, most striking of which is the zero order correlation between male and female siblings and the marked difference between the male parent-offspring and the female parent-offspring correlations. It seems most reasonable, at the moment, to assign these differences to peculiarities of the sample rather than to set up genetic hypotheses in explanation. The midparent-offspring correlations suggest a blending type of heredity to be operative, partly at least, in the production of eye color. There is no evidence in the correlations suggestive of sex linkage, of maternal influence (contrariwise paternal influence is suggested), or of the dominance of brown over nonbrown. The analysis of association by the chi-square method substantiates the findings of correlation. Differences between χ^2 values and the derived C values are less striking than those of correlation.

The question of dominance of brown over nonbrown may be tested by examining the offspring of completely brown-eyed parents. Fourteen parents, four male and ten female, rated grade 7, were paired in the seven possible mating combinations. In the first group (PP=1×7) three of the brown-eyed parents are females and one a male. All of the male offspring, three at grade 2, one at grade 4, and one at grade 7, have brown-eyed mothers; the female offspring of grade 2 has a brown-eyed father. Two families are shown with parentage 2×7; in one the father is graded 7 and his son 6; in the other the mother is at 7, two sons at 1, one son at 2, and one daughter at 6. Three families containing four male and one female children have parents 3×7. In one family father and son are 7, in another the mother is 7 and the daughter 5, and in the last the mother is 7 with three sons at grades 1, 2, and 5, respectively. In the 4×7 matings the female parent is at 7 in each case and one male offspring is at 2 and one female offspring at 4. There are two two-child families with parentage 5×7. In the first the father is brown-eyed with daughters grading 2 and 7 and in the second the mother is brown-eyed with sons at 5. Mother and son are grade 7 in the only family of parentage 6×7.

There can be no doubt, in view of the distribution of brown pigment among children who have one brown-eyed parent, that there is no simple dominance of brown over nonbrown in the inheritance of human eye color.

From the details cited above, and further verified by an examination of the complete data presented in Table III, it is equally clear that the postulation of sex linkage, of sex influence, or of maternal influence is not warranted.

No further analysis needs be presented to test a single gene hypothesis. Examination of Table II fails to reveal any evidence of segregation in any systematic proportion such as would be necessary to support a single gene proposition. One may postulate with assurance that the inheritance of brown versus nonbrown eye color is controlled by multiple factors and leave for further research the ascertainment of the number and mode of operation of the several genes involved.

TABLE III

DETAILS OF EYE-COLOR GRADE FOR BROWN IN PARENTS AND OFFSPRING ARRANGED BY FAMILIES ACCORDING TO GRADES OF PARENTS

The age in years follows the eye-color grade of each child; A indicates Adult

Heredity Clinic Number	Father	Mother	Sons	Daughters
32	1	1	1(13)	
43	1	1		1(9)
.....	1	1		1(11) 1(3)
1	1	1	1(19) 1(17)	3(21) 2(13)
			1(15) 1(10)	
72	1	1	1(11) 1(3)	1(14)
22a	1	1	1(A) 1(A)	1(A) 1(A)
				1(A) 1(A)
40	1	2		2(13)
16a	2	1	1(A)	
54	2	1	2(19)	
59	1	2		1(18)
7	1	2	1(12)	1(15) 1(15)
16b	1	2	2(10)	2(8)
.....	1	2		1(13) 2(11)
76	1	2	1(9)	2(5)
65	2	1	1(13)	2(12) 2(10)
				2(8) 2(6)
68	1	2	2(18) 1(15)	3(11) 2(4)
			2(14) 1(12)	
30	3	1	1(9) 2(7)	
.....	1	3	3(10)	
19	3	1	2(9) 1(5)	1(18)
22b	1	3	1(A) 3(A)	2(A)
			2(A) 3(A)	
39	4	1		2(12)
46	1	4	4(13)	
93	4	1		4(8)
15	1	4	2(8)	2(11)
.....	4	1	2(14)	1(A)
22c	1	4	1(9)	1(5)
73	1	4	1(3)	1(5)
70	4	1	5(17) 5(14)	1(10) 1(4)
83	1	4	2(12)	1(9) 1(5)
327	5	1	5(12)	
111	1	5	1(9)	
78	1	5		2(9) 2(7)
3	1	6	2(13)	1(9)
.....	1	6	1(10) 2(7)	5(9)
26	1	6	2(13)	1(8)
35	7	1		2(11) 2(11)
37	1	1		2(10)
107	1	7	7(13)	
.....	1	7	2(7)	4(5)
47	2	7	2(11) 2(2)	
49	2	2	1(11)	
51	2	2		2(11)
45	2	2		2(11)
86	2	2		2(12)
20	2	2		2(7)
14	2	2	1(8) 2(3)	
11	2	2	1(11) 2(10)	
9	2	2	1(11)	1(13)
			2(11)	2(4)

TABLE III—(Cont.)

Heredity Clinic Number	Father	Mother	Sons	Daughters
24	2	2	2(10)	5(8)
80	2	2	2(11)	1(9)
2	2	2	2(12)	2(18) 3(16) 2(14)
.....	2	2	1(10) 2(5) 1(3)	
62	2	2		4(10) 2(6)
66	2	2	2(11)	1(13) 2(10)
34	3	2		3(11)
42	2	3		3(8)
91	2	3	3(12)	
99	2	3	3(9)	
60	3	2	2(10)	2(8)
23	3	2		2(9) 2(7)
63	2	3	3(4)	2(12) 3(10) 3(8) 1(6)
31	2	4	1(11)	
56	4	2	2(11)	
57	4	2	6(14)	
6	2	4	2(7)	5(10) 4(5)
12	4	2	3(9)	4(7)
8	2	4	4(14)	7(12)
.....	4	2	4(8) 5(6)	1(11) 1(3)
.....	4	2	3(9) 3(7) 5(6)	
75	4	2		6(18) 1(13)
29	5	2	5(14)	
33	5	2	3(10)	
.....	2	5		2(13) 2(9)
79	2	5		3(13) 4(11) 3(8)
38	2	6		2(12)
21	2	6	3(13)	4(15)
28	7	2	6(9)	
67	2	7	2(8) 1(7)	6(6)
			1(3)	
48	3	3	5(9)	
61	3	3	4(11)	
88	3	3		4(11)
90	4	3		3(10)
27	4	3	5(14) 4(12)	1(8)
17	4	3	3(6)	6(9)
80	3	4	4(9) 4(4)	
50	3	5		1(6)
53	5	3		4(11)
55	5	3		2(13)
.....	3	5		3(20)
4	3	5	2(15) 2(13)	3(11)
.....	3	7		5(14)
64	7	3	7(14)	
5	3	7	1(10) 2(8) 5(6)	
13	4	4	6(12) 4(7) 5(11)	2(9)
.....	4	4		5(13)
41	5	4		1(9)
92	4	5		
77	4	5	5(8) 5(5)	
71	5	4	5(14) 5(9)	5(11)

TABLE III—(Cont.)

DETAILS OF EYE-COLOR GRADE FOR BROWN IN PARENTS AND OFFSPRING ARRANGED BY FAMILIES ACCORDING TO GRADES OF PARENTS

Heredity Clinic Number	Father	Mother	Sons	Daughters
69	6	4	5(12) 6(10)	
44	4	7	2(13)	
85	4	7		4(10)
18	5	5	2(5)	6(9)
82	7	5		2(12) 7(8)
25	5	7	5(13) 5(10)	
36	6	7	7(13)	

SUMMARY

The inheritance of brown and nonbrown pigment has been studied quantitatively insofar as quantity may be appraised by visual techniques without the aid of specialized measuring tools.

The data were obtained from 107 families with a total of 212 children. The racial ancestry may be classified as North European.

The method of analysis was statistical, using correlation and χ^2 as the basic techniques.

The many sampling irregularities indicate the need for more extensive data.

A multiple factor type of inheritance of brown versus nonbrown eye-color is indicated.

Dominance of brown over nonbrown pigment, sex linkage, and sex influence are contraindicated.

